

LIFE HISTORIES AND DESCRIPTIONS OF ADULTS AND IMMATURE STAGES OF TWO CRYPTIC SPECIES, *ACIURINA FERRUGINEA* (DOANE) AND *A. MICHAELI*, NEW SPECIES (DIPTERA: TEPHRITIDAE), ON *CHRYSOTHAMNUS VISCIDIFLORUS* (HOOKER) NUTTALL IN SOUTHERN CALIFORNIA

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Abstract.—*Aciurina ferruginea* (Doane) and the newly described species, *A. michaeli* Goeden, are sympatric univoltine fruit flies that form different, distinct types of axillary bud galls on branches of high-elevation plants of *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. Both species heretofore were called *A. ferruginea*; however, the gall attributed to this species in the literature in actuality belongs to *A. michaeli*. Accordingly, the gall of *A. michaeli* is smooth and beaked apically; the gall of *A. ferruginea* is subspheroidal and covered by many thin, threadlike leaves, its shape apparently unlike other tephritid galls described to date. The adults of *A. michaeli* are described as having a wholly dark brown or dark reddish-brown scutellum that readily distinguishes them from *A. ferruginea* which have a yellow or reddish-yellow scutellum. The slightly sexually dimorphic, but otherwise indistinguishable, wing patterns of both species are described and illustrated. The egg, third instar, and puparium of *A. michaeli* and *A. ferruginea* are described, illustrated and compared. The first and second instars of *A. ferruginea* also are described and illustrated. The eggs of both species have long pedicels that allow respiration by embryos within egg bodies buried during oviposition in axillary buds covered by resin. The third instar of *A. michaeli* is pyriform with abdominal tergites III-VI protrudent; the third instar of *A. ferruginea* is oblong-ellipsoidal. The prothorax in *A. michaeli* lacks the verruciform sensilla that circumscribe the prothorax in *A. ferruginea* in a single row. The anterior thoracic spiracles in *A. michaeli* have three or four papillae; whereas, *A. ferruginea* have five papillae. The puparium of *A. michaeli* is pale yellow; that of *A. ferruginea* is light to reddish-yellow.

Key Words: Insecta, *Aciurina*, *Chrysothamnus*, biology, galls, taxonomy of adults and immature stages, parasitoids

The five *Aciurina* spp. (Diptera: Tephritidae) forming galls on *Chrysothamnus nauseosus* (Pallen) Britton and *C. viscidiflorus* (Hooker) Nuttall (Asteraceae) in southern California were studied by us to expand upon the seminal studies of Wangberg (1981) in Idaho and to clarify certain of his findings as taxonomically interpreted by Steyskal (1984). This paper follows our published life history of *A. thoracica* Cur-

ran (Headrick and Goeden 1993), as second in a projected series of life histories to include at least three more southern California species of *Aciurina*. Herein, we distinguish a heretofore little known, cryptic, congeneric species of *Aciurina* that forms galls on the same host plant as *A. ferruginea* (Doane), that Wangberg (1981) called "*Aciurina* sp. B" and Steyskal (1984) suggested was *A. idahoensis* Steyskal. The bi-

ology and gall of *A. ferruginea* are re-described and the immature stages and adults of this species and the new species are comparatively described.

MATERIALS AND METHODS

Most field studies were conducted on *Chrysothamnus viscidiflorus* (Hooker) Nuttall (Asteraceae) South of Wongo Peak, along Horseshoe Meadow Road at Little Cottonwood Creek at 2810-m elevation, Inyo Nat. Forest, Inyo Co., in the southern Sierra Nevada Mountains. Samples of branches from individual plants that bore galls of *A. ferruginea* (as interpreted in the present paper) during previous years and contained overwintering eggs and larvae were collected on 14.viii.1993 and 18.ix.1993. Galls containing larvae and puparia of *A. ferruginea* were sampled from the same plants and others at this location during April–July, 1991–94. Additional collections of mature galls were made SE of Long Valley at 1730 m, in Kennedy Meadows at 1830 m, SE of Kennedy Meadows in Big Pine Valley, and S of Rattlesnake Meadow at 2160 m during July, 1991 and 1992. All four sites are located in the Sequoia Nat. Forest (N section) in Tulare Co. Galls of the new species described herein as *A. michaeli* were principally collected under the mistaken belief that they belonged to *A. ferruginea* as studied and its galls and biology described by Tauber and Tauber (1967) and Wangberg (1981). Branch samples bearing eggs and galls were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twelve and 14 ova dissected from mature females, 25 and five larvae, eight and two puparia of *A. ferruginea* and the new species of *Aciurina*, respectively, dissected from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). All other fully grown larvae and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and

held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM later were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials as well as field-swept adults were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991) for direct observations, videorecording, and still-photography of their courtship and copulation behavior to be reported elsewhere (Headrick and Goeden, unpublished data).

Plant names used in this paper follow Munz (1974); tephritid names follow Foote et al. (1993). Descriptions of the adults use the nomenclature of Foote et al. (1993); modified elements of the formats of Steyskal (1984), Hernández O. (1993), and Goeden (1993); and only flies individually reared from galls. Nomenclature used to describe the immature stages follows Goeden and Headrick (1990; 1991a, b; 1992), Headrick and Goeden (1990, 1991, 1993), and the telegraphic format of Goeden et al. (1993, 1994a, b). Means \pm SE are used throughout this paper. The holotype, allotype, and four individually reared paratypes of each sex of the new species, *A. michaeli*,

have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Two additional, individually reared paratypes of each sex also were deposited in the collection of the California Academy of Sciences (CAS). One male and two female paratypes reared by J. A. Wangberg were deposited in the W. F. Barr Entomological Museum (WFBARR), University of Idaho, Moscow, along with other material on loan viewed, confirmed, and identified during the present study. Seven remaining female paratypes and voucher specimens of swept adults of *A. michaeli* not designated as paratypes and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT. Two each, individually reared males and females of *A. ferruginea* used for comparison with *A. michaeli* were also deposited in the USNM and CAS collections, and in the James Entomological Collection at Washington State University, Pullman (WSUP) in gratitude for the loan of the holotype of the former species.

RESULTS AND DISCUSSION

Taxonomy

Adult.—The new species described below is very similar to *Aciurina ferruginea* in appearance, and probably resides under this name in most collections, as it did with RDG until comparison was made of specimens reared from two different morphs of galls collected together from high-elevation demes of *Chrysothamnus viscidiflorus* in the southern Sierra Nevada Mountains. The new species with a mostly dark brown scutellum is readily distinguished from *A. ferruginea* which has a yellow or reddish-yellow scutellum. This is the main morphological difference between the adults of these two cryptic species, otherwise distinguished by their distinctive galls. Accordingly, the following key to replace couplet 8 in the key to North American species of

Aciurina in Foote et al. (1993) [couplet 15 (16) in Steyskal (1984)] enables one to distinguish these closely related species (parenthesized additions and deletions are those of RDG):

- 8. Cell r_{4+5} wholly brown or with small rounded hyaline spot near wing tip adjacent to vein M; cell c broadly hyaline distally, with transverse median brown bar . . . ; cell dm with preapical hyaline spot (usually) not extending to veins at sides of cell (but sometimes barely touching vein R_{4+5} anteriorly) 8a
- 8a. Scutellum entirely dark brown or occasionally dark reddish brown with yellow or reddish yellow apex *michaeli* Goeden n. sp.
- Scutellum all yellow, reddish-yellow, or broadly so along entire posterior margin *ferruginea* (Doane)
- Cell r_{4+5} with preapical hyaline mark occupying at least half of width of cell.
- sometimes with an additional subbasal hyaline mark . . . ; cell c with distal dark area . . . or its apex sometimes largely hyaline 9

***Aciurina michaeli* Goeden, NEW SPECIES**

Aciurina ferruginea: Tauber and Tauber 1967: 907 (reproductive behavior, biology, gall photo). Wangberg 1981: 712–714 (gall description, biology, parasitoids).

Male (Holotype).—*Head*: Light to golden yellow; occiput dark brown and covered with fine grey pollinosity. Three pairs of frontal bristles; two pairs of orbital bristles; inner vertical bristles and ocellar bristles well developed and light brown; other bristles wholly or basally white or light yellow.

Thorax: Dark brown, mesonotum covered with fine grey pollinosity and many prominent, pale to golden yellow setulae posteriorad as far as and including all but shiny, posterior margin of dark brown scutellum. Mediotergite dark brown, shiny medially, grey pollinose dorsally and laterally. All of the following bristles are present and brown: One pair of postpronotals; scapular bristles indistinguishable from microtrichia or absent; one pair of postsutural dorsocentrals slightly posteriorad of presutural supra-alars, at one-fourth the distance to the supra-alar bristles; two pairs of notopleurals; one pair each of post-alars, intra-alars,

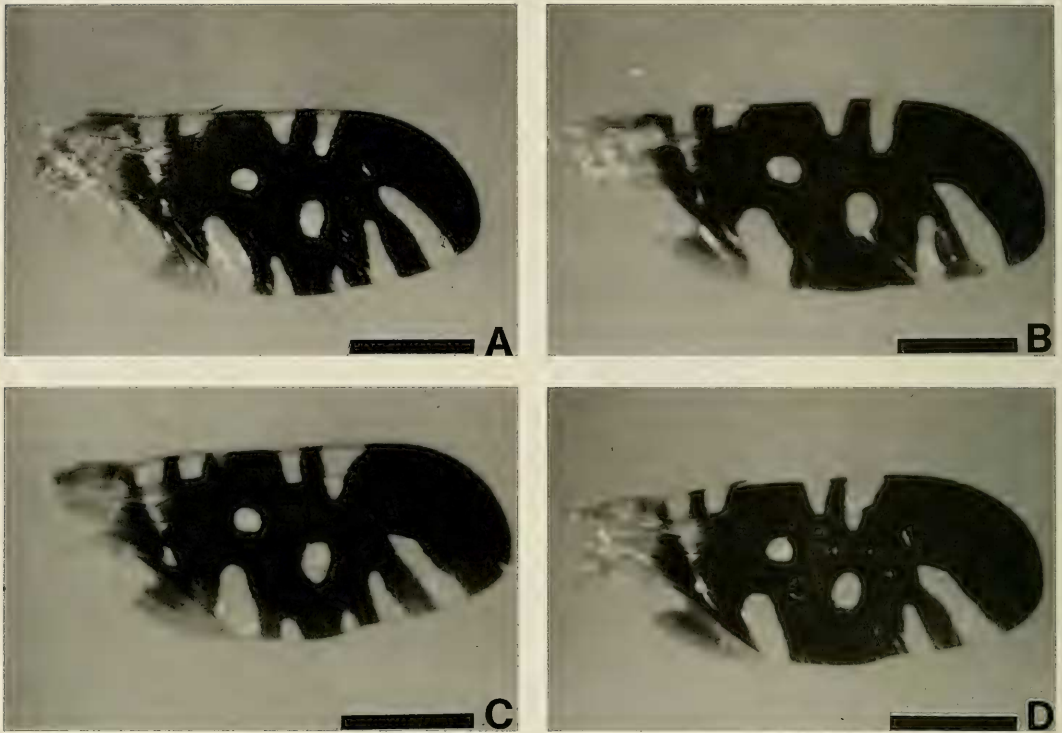


Fig. 1. Excised right wings of *Aciurina michaeli* (A) male, (B) female; and *A. ferruginea* (C) male, (D) female. Bar = 1 mm.

and acrostichals; scutellum with one pair of basal, prominent, scutellar bristles; katepisternal bristles well developed. Coxae, femora, tibiae, and tarsi yellow; fore femora twice as thick as mid- and hind femora and bearing loose "comb" of long, anteroventral setae. Wings (Fig. 1A) mostly dark brown with marginal hyaline incisions and internal marks as follows: cell bc wholly hyaline; cell c broadly hyaline distally, with transverse median brown bar; cell r_1 with two triangular, hyaline spots along costa, the proximal spot extending to vein R_{2+3} , the distal spot to vein R_{4+5} ; cell r_{4+5} wholly brown with a distinct bulla; cell dm with preapical hyaline spot not extending to vein CuA_1 , but in right wing, not left wing, just touching vein M; cell m with median hyaline, wedge-shaped stripe reaching vein M and sub-basal, wedge-shaped spot two-thirds as long; cell br with prominent, round or oval, preapical spot; cell cua_1 with three

marginal incisions, apical incision short and hugging vein CuA_1 , central narrow incision not reaching CuA_1 ; and prominent basal incision starting at vein $A_1 + CuA_2$ extending anteriorly to or nearly to CuA_1 .

Abdomen: Shiny, dark brown, variously marked with reddish-brown dorsoanteriorly; pleura yellow, dark brown ventrally, epandrium black; tergum sparsely covered with fine, light or dark microtrichia.

Female (Allotype).—Head: Like δ . **Thorax:** Like δ , but mediotergite black. Coxae, femora, tibiae, and tarsi reddish-yellow; fore femora unthickened. Wings like δ , but dimorphic, as cell cua_1 usually with only one marginal, hyaline incision (Fig. 1B). Abdomen with oviscapae shiny black, funnel-shaped, stout.

Variation. Heads of some δ paratypes are fuscous, with reddish-brown or light brown bristles; posterior orbital bristles sometimes lighter, shorter, and thicker than

anterior pair. Thorax lengths of 7 ♂ averaged 1.39 ± 0.033 (range, 1.30–1.52) mm. Microtrichia, like thorax, sometimes fuscous and reaching posteriorly only to base of scutellum; scutellum of ♂ paratype from Idaho reddish-brown with yellow brown apex. Mediotergite sometimes black; coxae, femora, tibiae, and tarsi sometimes fuscous. The distal hyaline spot arising on costa of 2 ♂ paratypes does not reach vein R_{4+5} ; the preapical hyaline spot in cell dm not touching vein M in all ♂ paratypes (Fig. 1A). Sub-basal hyaline spot in cell m, keyhole-shaped instead of wedge-shaped in 2 ♂ paratypes. Central narrow hyaline incision in cell m rarely absent. Abdomen also wholly dark brown or black dorsally and yellow, reddish-yellow, or partly black ventrally.

Coloration of ♀ paratypes as holotype and ♂ paratypes, except scutellum of 1 ♀ from California with reddish-yellow apex; 2 ♀ from Idaho with reddish-yellow scutellum, including apex, but reddish-brown laterally on posterior margin. Proximal hyaline spot extending only halfway across cell r_1 and distal spot across only anterior fourth of same cell in 1 small ♀ paratype; central incision in cell cua, represented by small, hyaline, premarginal spot in 4 ♀ paratypes. Thorax lengths of 14 ♀ averaged 1.66 ± 0.05 (range, 1.10–2.00) mm; oviscapces averaged 0.304 ± 0.007 (range, 0.275–0.369; $n = 13$) times as long as rest of abdomen. Tergite (T)1 black, T2 black anteriorly or T2 to T6 reddish-brown, or T6 with pair of black spots or nearly all black.

Diagnosis: The main morphological character separating the adults of *A. michaeli* from *A. ferruginea* is the color of the scutellum as described above. Both species are distinguished from other North American species of *Aciurina* by having cell r_{4+5} wholly brown, or according to Foote et al. (1993), this cell may sometimes bear a small rounded hyaline spot near wing tip adjacent to vein M (but see discussion below).

Types: Holotype, male, Middle Canyon,

2690 m, E of Boundary Peak in the White Mountains (just E of CA border), Inyo Nat. Forest, Esmeralda Co. Nevada; 10.vi.1987; R. D. Goeden, coll.; reared from gall on *C. viscidiflorus* mounted with fly (USNM); allotype, female, same data as holotype (USNM). Paratypes: NEVADA: 3 ♂ and 7 ♀; same data as holotype (3 ♂ and 4 ♀ to USNM, 2 ♀ to CAS). IDAHO: 1 ♂ and 2 ♀; 15 mi SW Rogerson, Twin Falls Co.; 25.vii.1975; J. K. Wangberg (717-34); re. from galls on *C. viscidiflorus* (galls mounted with specimens) (WFBARR). Also individually reared by R.D.G. and J.A.T. from galls on *C. viscidiflorus* in CALIFORNIA: 2 ♂ and 2 ♀; Rodeo Flat, 2200 m, Sequoia Nat. Forest, Tulare Co.; 14.vi.1990 (2 ♂ to CAS). 1 ♂ and 3 ♀; S of Wongo Peak at Little Cottonwood Creek on Horseshoe Meadow Road, 2810 m, Inyo Nat. Forest, Inyo Co.; 23.vi.1992 (1 ♂ to USNM). 1 ♀; Big Pine Meadow, along Kennedy Meadow Road, Tulare Co.; 14.vi.1993 (remaining 7 ♀ paratypes held in research collection of RDG).

Additional swept specimens examined and reared specimens mounted without galls examined and not designated as paratypes, included from CALIFORNIA: 1 ♂; Mahogany Creek, Sequoia Nat. Forest (N section), Tulare Co.; 25.vii.1984. 9 ♂ and 3 ♀ at 3140 m and 3 ♂ and 1 ♀ at 3440 m on White Mountain, Inyo Nat. Forest, Inyo Co.; 19.ix.1987. 10 ♂ and 4 ♀; above and W of Wyman Canyon at 3020 m on White Mountain, Inyo Co., Inyo Nat. Forest; 27.vii.1989. 1 ♀; N of Mono Lake, 1990 m, Mono Co.; 31.vii.1992. 1 ♂; Mormon Meadow along Clearwater Creek and road to Bowie, 3050 m, Mono Co.; 31.vii.1992. 8 ♂; S of Wongo Peak at Little Cottonwood Creek on Horseshoe Meadow Road, 2685 m, Inyo Co.; 31.vii.1992. 9 ♂ and 5 ♀; S of Wongo Peak at Little Cottonwood Creek on Horseshoe Meadow Road, 2810 m; 17.viii.1994. IDAHO: 1 ♂; 7 mi NW of Weston, Franklin Co.; 3.viii.1958; A. L. Gittens, coll. 7 ♂ and 1 ♀; 10 mi S of Gilmore, Lemhi Co.;

24.vii.1959; H. C. Manis, coll. 2 ♀; 2 mi SW of Rogerson, Twin Falls Co.; 28.vii.1965. 1 ♀; 19 mi W of Swan Valley, Bonneville Co.; 19.vii.1966; L. S. Hawkins, coll. 2 ♂; 2 mi W of Carey, Blaine Co.; 29.vi.1974; L. S. Hawkins, coll. 1 ♂ and 2 ♀; 12.5 mi SE Oakley, Cassia Co.; 17.vii.1975; J. K. Wangberg (706-34); re. from galls on *C. viscidiflorus*. 4 ♂ and 1 (probable) ♀ (abdomen missing); 7 mi NE Craters of the Moon Nat. Mon., Butte Co.; 23.vii.1975; J. K. Wangberg (715-34); re. from galls on *C. viscidiflorus*. 3 ♂ and 4 ♀; 20 mi SW Rogerson, Twin Falls Co.; 13.vii.1978; J. K. Wangberg (698-34); re. from *C. nauseosus*. OREGON: 1 ♀; Redmond; 6.viii.1939; Schuh & Scott, coll. 1 ♂; Klamath Falls; 13.viii.1954; Toby Schuh, coll. 4 ♂; 2.5 mi E Sheaville, Malheur Co.; 24.vii.1966 (2 ♂) and 13.vii.1966 (2 ♂); E. J. Allen, coll. 2 ♂; Riggins, Idaho Co.; 31.vii.1967. WASHINGTON: 1 ♂ and 1 ♀; 2 mi. E. Washucha, 1000 ft. Adams Co.; 24.viii.1976; W. Turner, coll.; *Chrysothamnus*. 1 ♀; Hanford Site, ALE. radio telescope N46°23.549'W119°35.125', Benton Co.; 12.ix.1994; R. S. Zack, coll. 2 ♂; Hanford site, ALE. radio telescope, N46°23.549'W119°35.125', Benton Co.; 18.viii.1994; R. S. Zack, coll. 1 ♂; Hanford Site, ALE. Rattlesnake Ridge, spring, N46°24.391'W119°36.312', Benton Co.; 19.viii.1994.

Etymology: *Aciurina michaeli* is named for my son, Michael, who along with his mother, my wife Joan (Goeden 1993), and his two sisters (for whom my next two new species will be named), are continuing sources of pride in their accomplishments and the principal foci of my non-entomological life.

Discussion: *Aciurina michaeli* does not belong to the *Aplopappi* group, i.e. *A. mexicana* (Aczél), *A. mixteca* Hernandez O. (1993), *A. thoracica* Curran, and *A. aplopappi* (Coquillett), designated by Steyskal (1984), and adopted by Foote et al. (1993) and added to by Hernandez O. (1993). Examination of the holotype of *A. ferruginea*

confirmed that this specimen, which lacks an abdomen, right middle leg, and both hind legs, and from which the right wing was removed and slide mounted (Zack 1984), nevertheless, has a yellow scutellum. Furthermore, the sex of the holotype, which Doane (1899) noted had "yellow on the posterior margin of the scutellum", but which lacked an abdomen, probably is a male, judging from the three marginal incisions present in cell cua_1 of the left wing remaining on this specimen [Plate III, Fig. 6 in Doane (1899); Zack 1984] and the slide-mounted right wing (Zack 1984).

The key character involving scutellum color so useful for separating California *A. ferruginea* from *A. michaeli* may show regional variation, as indicated by the three reared paratypes from Idaho. Also, among specimens swept from *C. viscidiflorus* in southern California 40 keyed to *A. ferruginea* and 55 to *A. michaeli* (1: 1.4); whereas, among swept or reared specimens mounted without galls in material examined from Idaho, 139 keyed to *A. ferruginea* but only 37 to *A. michaeli* (3.8:1). This predominance of *A. ferruginea* contradicts Wangberg's (1981) description of the galls of *A. michaeli* (identified by him as those of *A. ferruginea*) as being "commonly collected"; whereas, adults of *A. ferruginea* (his *Aciurina* sp. B) were "... rarely reared in the laboratory and not observed in the field" and the galls as "... collected at 3 widely separated localities" (see further discussion below on identity and descriptions of galls of these tephritids). Future examination of fly specimens from Idaho and elsewhere carefully mounted with galls from which each was individually reared, as done with specimens from southern California in the present study, may clarify this issue. That certain *Aciurina* spp. show regional differences in wing patterns will be documented in our forthcoming paper on *A. idahoensis* (Goeden and Teerink, unpublished data).

Examination of the swept specimens described above yielded none from California,

Idaho, Oregon, or Washington with a small round hyaline spot near the wing tip in cell r_{4+5} adjacent to vein M, as noted in the keys of Steyskal (1984) and Foote et al. (1993). Specimens bearing this spot probably are variants of *A. trixa* Curran, which Steyskal (1984) synonymized with *A. bigeloviae* (Cockerell), but Dodson & George (1986) resurrected [correctly so, as the two species are, indeed, morphologically and biologically distinct, and the former is the most common species on *C. nauseosus* in southern California (Headrick, Goeden, and Teerink, unpublished data)]. Doane (1899) did not mention or illustrate any such spot, nor does the holotype bear same. However, two of 41 (5%) swept males from California did have a small, subbasal hyaline spot in cell r_{4+5} . Additionally, in 17 of 41 (40%) swept specimens from California, including the preceding two males, the preapical hyaline spot in cell dm extended to and barely touched vein M, also contrary to the keys of Steyskal (1984) and Foote et al. (1993) (also see note on this character in the redescription of *A. ferruginea* below).

Differences in the immature stages and galls of *A. michaeli* and *A. ferruginea* described below further confirm the separate identities of these two species. I take this opportunity to redescribe *A. ferruginea* from a series of 21 ♂ and 14 ♀ individually reared from galls in comparison to the preceding description of *A. michaeli* to supplement the brief description which Doane (1899) based on a single damaged specimen.

Aciurina ferruginea (Doane)

Aciura ferruginea Doane 1899: 182 (holotype, male, WSUP; Pullman, Wash.).

Aciurina ferruginea (Doane): Curran, 1932: 10.

Aciurina sp. B of Wangberg 1981: 722 (gall photo), 727–728 (host plants, gall description, biology).—Steyskal 1984: 595 (revision).

Tephrella ferruginea (Doane): Bates, 1935: 109.

Head: As described above for *A. michaeli*, but generally lighter in color with golden yellow setae and bristles, or the latter brown.

Thorax: Thorax of 21 ♂ averaged 1.54 ± 0.02 (range, 1.36–1.68) mm in length; of 14 ♀, 1.8 ± 0.03 (range, 1.66–2.02) mm in length; dark brown, mesonotum covered with fine grey pollinosity and many, prominent, reddish-yellow or golden setulae posteriorad as far as and including all but posterior margin of scutellum. Scutellum pale yellow to reddish-yellow entirely, or at least along its entire posterior margin. Setae as described for *A. michaeli*. Coxae, femora, tibiae, and tarsi yellow or reddish-yellow like *A. michaeli*. Wings (Fig. 1C, D) as described for *A. michaeli*, but pattern more uniform throughout individuals examined. One reared female had a small subbasal hyaline spot in cell r_{4+5} of one wing. In three of 31 (14%) swept specimens from California, the preapical hyaline spot in cell dm extended to and barely touched vein M. Moreover, the apical incision in cell cua₁ was absent in all 14 reared ♀ and all 9 swept ♀ from California. One reared ♀ and one swept ♀ from California had a central medial incision and the former ♀ had this incision reduced to a small hyaline submarginal dot. Therefore, like *A. michaeli*, this character provides evidence of slight sexual dimorphism in wing patterns, heretofore unreported among North American *Aciurina* spp. (Steyskal 1984, Foote et al. 1993), but strongly developed in at least two additional California species currently under study (Goeden unpublished data).

Abdomen: Shiny, mostly reddish-yellow, with T5 sometimes wholly or laterally black, and epandrium always black, tergum sparsely covered with fine, light or dark microtrichia. Female with oviscapae shiny black, funnel-shaped, stout, 0.345 ± 0.008 (range, 0.315–0.380; $n = 7$) times as long as rest of abdomen; T1 to T6 reddish-brown.

Of 31 ♂ and 8 ♀ swept specimens from California, 12 ♂ from White Mountain had

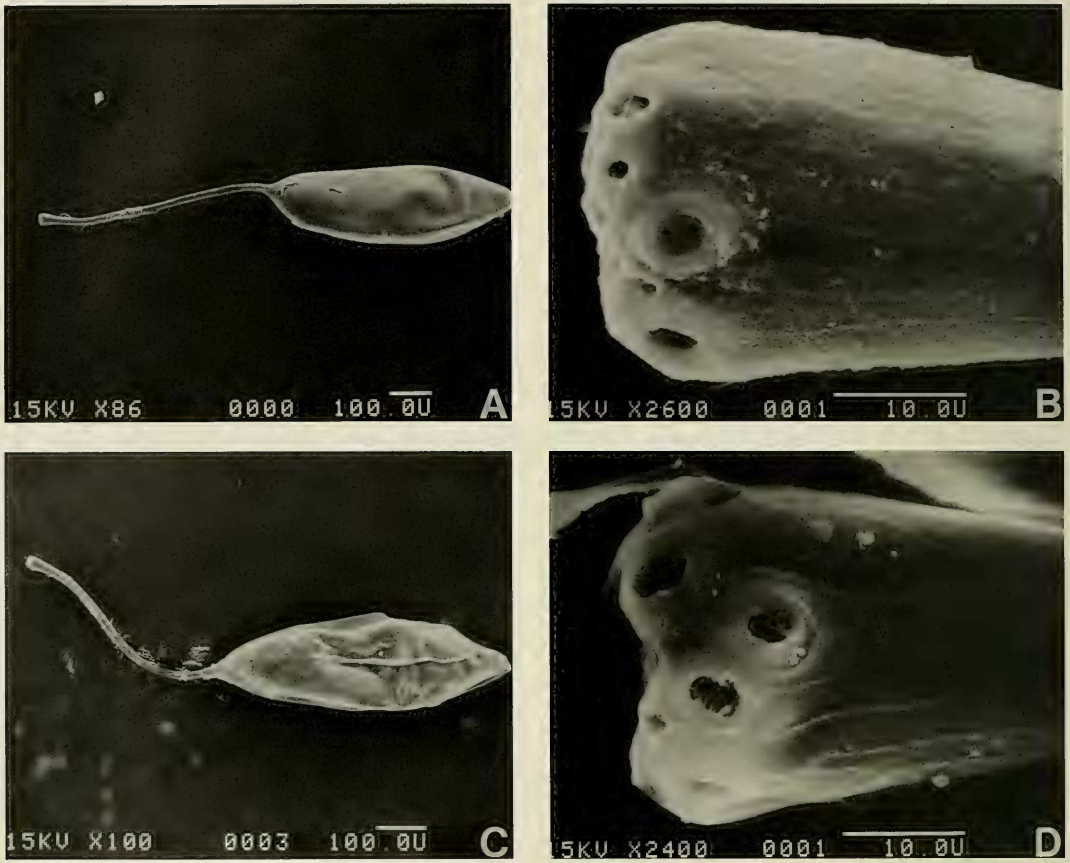


Fig. 2. Eggs of *Aciurina michaeli* and *A. ferruginea*: (A) egg of *A. michaeli*, (B) apex of pedicel of *A. michaeli* egg, (C) egg of *A. ferruginea*, (D) apex of pedicel of *A. ferruginea* egg.

all-black abdomens; whereas, 19 ♂ from the study site S of Wongo Peak had abdomens ranging from all-black to nearly all reddish-brown except for a black epandrium. Therefore, the color of the abdomens of the males of *A. ferruginea* like *A. michaeli* is quite variable. The lack of black abdomens among reared males of *A. ferruginea* from the study site S of Wongo Peak also indicates that the patterns of color on their abdomens vary within and among local fly populations. Five of six females of *A. ferruginea* swept on White Mountain had abdomens all reddish-brown except for black oviscapes and limited darkening on T1 on two, but the remaining female from the same mountain had a nearly black ab-

domen. The only female swept at the Wongo Peak site was as described above.

Comparisons of Immature Stages.—*Egg*. Fifteen ova of *A. michaeli* (Fig. 2A) were white, opaque, smooth; with an elongate-ellipsoidal body, 0.60 ± 0.004 (range, 0.56–0.62) mm long, 0.19 ± 0.005 (range, 0.16–0.24) mm wide, smoothly rounded at tapered posterior end; and with an elongate, anterior pedicel, 0.46 ± 0.016 (range, 0.36–0.56) mm long, 0.02 mm wide medially, and 0.04 mm wide at knoblike, anterior apex (Fig. 2B). Twenty-five ova of *A. ferruginea* with similar habitus (Fig. 2C); body 0.62 ± 0.006 (range, 0.58–0.66) mm long, 0.21 ± 0.003 (range, 0.20–0.24) mm wide; pedicels 0.59 ± 0.005 (range, 0.54–

0.62) mm long, 0.02 mm wide medially, and 0.04 mm wide apically (Fig. 2D).

These descriptions agree with the photo and description of the egg of what Tauber and Tauber (1967) reported as *A. ferruginea*, and may, indeed, refer to this species because of the mean and ranges for the lengths of the pedicel that they reported, i.e. 0.62 (range, 0.58–0.65; $n = 4$) mm. However, the eggs of *A. ferruginea* and *A. michaeli* differ strikingly from the short-pedicelled, partly reticulated egg of *A. thoracica* described by Headrick and Goeden (1993). As noted above, *A. thoracica* belongs to a different species group, the *Aplopappi* of Steyskal (1984). The egg body of the stalked egg of *Paracantha gentilis* Hering (Headrick and Goeden 1990) is twice as long on average, and its pedicel is more than four times longer (about 2.5 times the length of its egg body) than eggs of *A. ferruginea* and *A. michaeli*.

Third instar: Third instar of *A. michaeli* superficially smooth, pyriform, tapering anteriorly, rounded posteriorly, abdominal segments III–V enlarged dorsally, minute acanthae ventrolaterally along intersegmental lines (Fig. 3A); gnathocephalon conical, flattened apically, rugose pads laterad of mouth lumen; elongated petals dorsad of mouth lumen (Fig. 3B-1); paired dorsal sensory organs dorsomedial of anterior sensory lobes, each consisting of a dome-shaped papilla (Fig. 3B-2, C-1); anterior sensory lobes (Fig. 3B-3) bear the terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); stomal sense organs ventrolaterad of anterior sensory lobes, near mouth lumen (Fig. 3D-1); lateral (Fig. 3D-2) and ventrolateral sensilla (Fig. 3D-3) located laterad and ventrolaterad, respectively, of the rugose pads, each consisting of a verruciform sensillum; mouth hooks tridentate, teeth conical, sharply curved downward, medial tooth reduced (Fig. 3B-4, D-4); median oral lobe laterally flattened, tapering apically, attached to labial lobe (Fig. 3B-5); prothorax

smooth, minute acanthae ventrally (Fig. 3D-5); anterior thoracic spiracles dorsolaterad on posterior margin, consisting of three or four elongate-oval papillae (Fig. 3E); metathoracic lateral spiracular complex consists of an open spiracle (Fig. 3F-1) and a single verruciform sensillum (Fig. 3F-2); abdominal lateral spiracular complex consists of an open spiracle only; caudal segment bears the posterior spiracular plates (Fig. 3G); posterior spiracular plates bear three elongate-oval rimae ca. 0.038 mm in length (Fig. 3G-1), and four interspiracular processes with 1–3 branches each, longest measuring 0.01 mm (Fig. 3G-2); compound sensilla ventrad of posterior spiracular plate consist of a stelex sensillum (Fig. 3H-1) and a tuberculate, medusoid chemosensillum (Fig. 3H-2).

Third instar of *A. ferruginea* superficially smooth, oblong-elliptical, dorsally and ventrally rounded, minute acanthae ventrally (Fig. 4A); gnathocephalon conical, flattened apically, serrated rugose pads laterad of mouth lumen (Fig. 4B-1); paired dorsal sensory organs dorsomedial of anterior sensory lobes, each consisting of a dome-shaped papilla (Fig. 4B-2, C-1); anterior sensory lobes bear the terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4) and supralateral sensory organ (Fig. 4C-5); stomal sense organs ventrolaterad of anterior sensory lobes, near the mouth lumen (Fig. 4B-3); lateral (Fig. 4B-4) and ventrolateral sensilla (Fig. 4B-5) located laterad and ventrolaterad of rugose pads, respectively, each consisting of a verruciform sensillum; mouth hooks tridentate, medial tooth reduced, teeth stout, conical (Fig. 4D-1); median oral lobe laterally flattened, tapering anteriorly, attached to labial lobe (Fig. 4D-2); labial lobe bears two pore sensilla anteriorly (Fig. 4D-3); prothorax smooth, minute acanthae ventrally, single row of verruciform sensilla circumscribe prothorax; anterior thoracic spiracles dorsolateral on posterior margin, each consisting of five oval papillae (Fig. 4E); meso- and metatho-

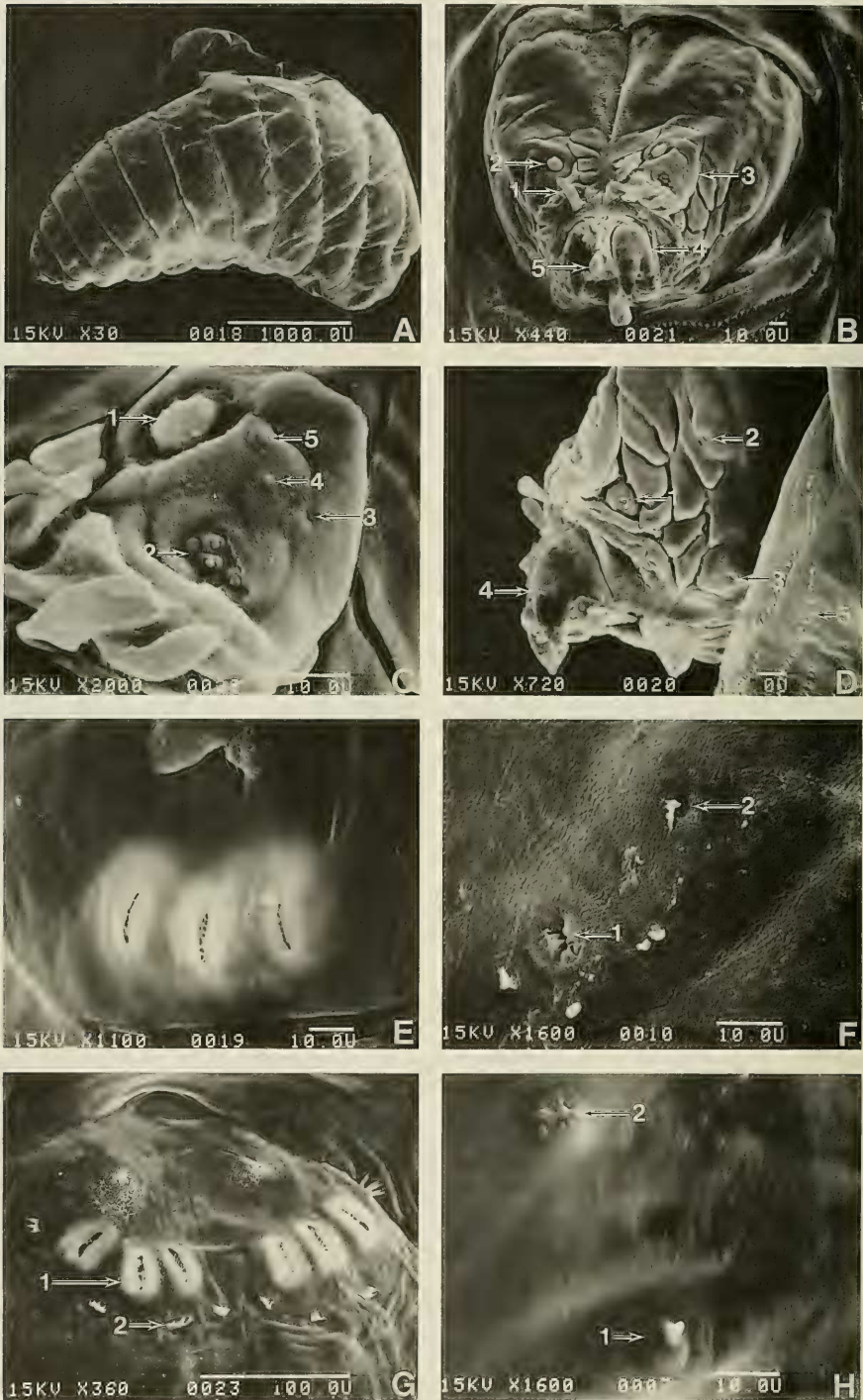


Fig. 3. Third instar of *Aciurina michaeli*: (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—elongated petals, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—mouth hooks, 5—median oral lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon, lateral view, 1—stomal sense organ, 2—lateral sensillum, 3—ventrolateral sensillum, 4—mouth hooks, 5—minute acanthae; (E) anterior thoracic spiracle;

racic lateral spiracular complexes consist of an open spiracle (Fig. 4F-1), and three verruciform sensilla (Fig. 4F-2); caudal segment bears the posterior spiracular plates (Fig. 4G); posterior spiracular plates bear three oval rimae, ca. 0.036 mm in length (Fig. 4G-1), and four interspiracular processes with 3–8 branches each, longest measuring 0.024 mm (Fig. 4G-2); two compound sensilla ventrad of posterior spiracular plates (Fig. 4G-3), consist of a tuberculate chemosensillum (Fig. 4H-1), and a raised verruciform sensillum with a central papilla (Fig. 4H-2) in one, and a tuberculate chemosensillum and stalex sensillum in the other; stalex sensilla surround margin of caudal segment in 2-dorsal, 4-ventral arrangement.

The habitus of the third instar *A. michaeli* differs dramatically from that of *A. ferruginea*. The abdominal segments III–V in *A. michaeli* are greatly expanded dorsally, forming a distinct hump. Wangberg (1981) suggested that the hump was used to move inside the gall cavity. No previously examined Tephritidae has displayed a similar habitus (Goeden and Headrick 1990, 1991a, b, 1992; Goeden et al. 1993, 1994a, b; Headrick and Goeden 1990, 1991). *Aciurina ferruginea* closely resembles *A. thoracica* in general habitus (Headrick and Goeden 1993). The gnathocephalon of *A. michaeli* and *A. ferruginea* are very similar to each other, with only slight differences in the shape of the rugose pads. The prothorax in *A. ferruginea* is circumscribed by a single row of verruciform sensilla, but *A. michaeli* lacks such verruciform sensilla. The prothorax in *A. thoracica* has two rows of verruciform sensilla circumscribing the prothorax (Headrick and Goeden 1993). *Aciurina michaeli* differs from *A. ferruginea* and *A. thoracica* in the number of papillae

in the anterior thoracic spiracles, three or four in *A. michaeli*, five in *A. ferruginea*, and four papillae each in *A. thoracica* (Headrick and Goeden 1993). The lateral spiracular complexes also differ among the three species. *Aciurina ferruginea* has three verruciform sensilla in the metathoracic lateral spiracular complex, *A. michaeli* has only one verruciform sensillum. *Aciurina thoracica* has one verruciform sensillum in the metathoracic lateral spiracular complex, but differs from *A. michaeli* in having one sensillum in the abdominal segments (Headrick and Goeden 1993). The caudal segment also differs slightly, the interspiracular processes have more individual branches in *A. ferruginea* than in *A. michaeli*, and stalex sensilla surround the caudal margin in *A. ferruginea*. *Aciurina thoracica* differs from *A. michaeli* and *A. ferruginea* in having very reduced interspiracular processes (Headrick and Goeden 1993).

Second instar: Second instar of *A. ferruginea* superficially smooth, oblong-elliptical, tapering anteriorly, rounded posteriorly, minute acanthae ventrally (Fig. 5A); gnathocephalon conical, rugose pads laterad of mouth lumen (Fig. 5B-1); petals dorsad of mouth lumen (Fig. 5B-2); paired dorsal sensory organs dorsomedial of anterior sensory lobes (Fig. 5B-3, C-1); anterior sensory lobes dorsolaterad of mouth lumen (Fig. 5B-4, C), bear the terminal sensory organ (Fig. 5C-2), pit sensory organ, lateral sensory organ (Fig. 5C-3), and supralateral sensory organ (Fig. 5C-4); stomal sense organs ventrolaterad of anterior sensory lobe, near mouth lumen (Fig. 5D-1); lateral (Fig. 5D-2) and ventrolateral (Fig. 5D-3) sensilla located laterally and ventrolaterally of rugose pads, respectively; mouth hooks bidentate, teeth conical, sharply pointed (Fig.

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(F) metathorax, lateral spiracular complex, 1—spiracle, 2—verruciform sensillum; (G) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process; (H) caudal segment, compound sensillum, 1—stalex sensillum, 2—tuberculate medusoid chemosensillum.

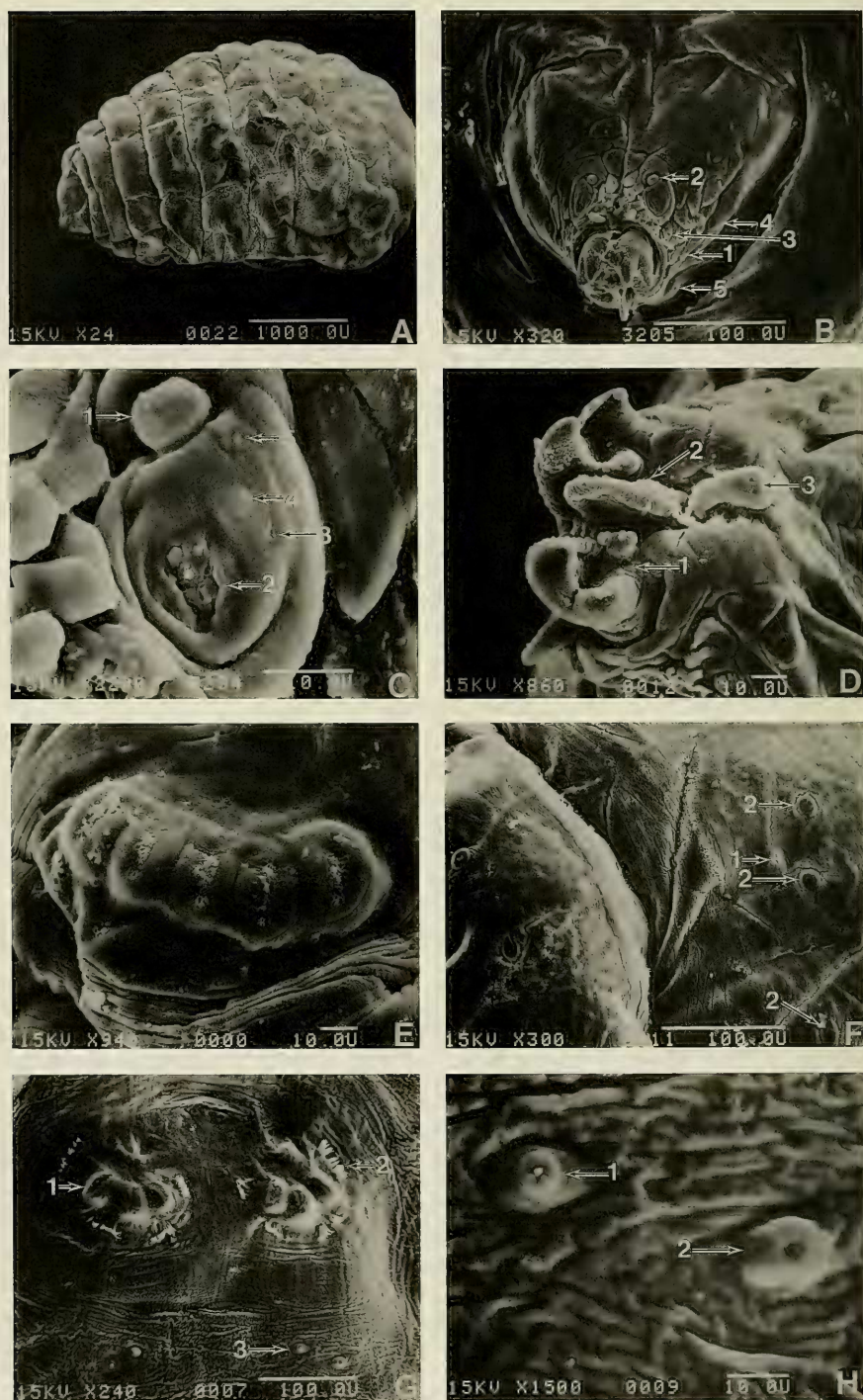


Fig. 4. Third instar of *Aciurina ferruginea*: (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—serrated rugose pads, 2—dorsal sensory organ, 3—stomal sense organ, 4—lateral sensillum, 5—ventrolateral sensillum; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon, ventral view, 1—mouth hooks, 2—median oral lobe, 3—labial lobe pore sensilla; (E) anterior thoracic spiracle; (F) mesothorax and metathorax, 2—median oral lobe, 3—labial lobe pore sensilla; (G) anterior thoracic spiracle, 1—dorsal sensory organ, 2—lateral sensory organ; (H) mesothorax and metathorax, 1—dorsal sensory organ, 2—lateral sensory organ.

5D-4); median oral lobe laterally flattened, attached to labial lobe (Fig. 5D-5); labial lobe bears two pore sensilla anteriorly (Fig. 5D-6); prothorax smooth, minute acanthae ventrally, single row of verruciform sensilla circumscribe prothorax; anterior thoracic spiracles dorsolaterad on posterior margin of prothorax, papillae indistinct (Fig. 5E); meso- and metathoracic lateral spiracular complexes consist of an open spiracle (Fig. 5F-1), and two verruciform sensilla (Fig. 5F-2); caudal segment bears the posterior spiracular plates (Fig. 5G); posterior spiracular plates bear three oval rimae, ca. 0.012 mm in length (Fig. 5G-1), and four, blade-like interspiracular processes with 2–4 branches each, longest measuring 0.009 mm (Fig. 5G-2); compound sensilla ventrad of posterior spiracular plates (Fig. 5G-3), consist of a stelex sensillum (Fig. 5H-1) and a tuberculate chemosensillum with a central papilla (Fig. 5H-2); stelex sensilla surround margin of caudal segment (Fig. 5G-4).

The second instar of *A. ferruginea* differs slightly from the third instar. Most morphological features of the second instar are similar in shape and placement to those of the third instar, but not as structurally distinct as on the mature larva. Only two verruciform sensilla were observed in the lateral spiracular complex of the second instar; this may be due to the wrinkled nature of the specimen examined. The caudal segment of the two instars differed slightly. The posterior spiracular plates in the second instar were closer together, with smaller rimae and interspiracular processes with fewer branches. The compound sensilla in the second instar consisted of tuberculate chemosensilla and stelex sensilla, but no verruciform sensilla as observed in the third instar.

First instar. First instar of *A. ferruginea*

superficially smooth, oblong-elliptical, tapering anteriorly, rounded posteriorly, minute acanthae ventrally (Fig. 6A); gnathocephalon conical, laterally flattened, smooth, lacking rugose pads (Fig. 6B); single pair of petals dorsad of mouth lumen (Fig. 6B-1); paired dorsal sensory organs dorso-mediad of anterior sensory lobes (Fig. 6B-2, C-1); anterior sensory lobes (Fig. 6C) bear the terminal sensory organ (Fig. 6C-2), pit sensory organ (Fig. 6C-3), lateral sensory organ (Fig. 6C-4), and supralateral sensory organ (Fig. 6C-5); stomal sense organs indistinct, ventrolaterad of anterior sensory lobes (Fig. 6B-3); lateral and ventrolateral sensilla indistinct; mouth hooks bidentate, teeth conical, rounded apically (Fig. 6B-4); median oral lobe laterally flattened (Fig. 6B-5); prothorax smooth, minute acanthae ventrally; anterior thoracic spiracles absent; lateral spiracular complex not observed; caudal segment bears the posterior spiracular plates (Fig. 6D-1); posterior spiracular plates bear two, indistinct rimae (Fig. 6E-1), and four, spine-like interspiracular processes, longest measuring 0.008 mm (Fig. 6E-2); compound sensilla ventrad of posterior spiracular plates (Fig. 6D-2, E-3), consist of a stelex sensillum (Fig. 6F-1) and a tuberculate medusoid chemosensillum (Fig. 6F-2); two stelex sensilla dorsolaterad of posterior spiracular plates (Fig. 6D-3).

The morphological features of the first instar of *A. ferruginea* are much less distinct than those of the second and third instar. The gnathocephalon in the first instar lacks rugose pads, has a single pair of dorsal petals, and the stomal sense organs, lateral and ventrolateral sensilla are indistinct. The respiratory system undergoes major morphogenesis between the first and second instars. In the first instar, the anterior spir-

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lateral spiracular complex, 1—spiracle, 2—verruciform sensilla; (G) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process, 3—compound sensillum; (H) caudal segment, compound sensillum, 1—tuberculate chemosensillum, 2—verruciform sensillum.

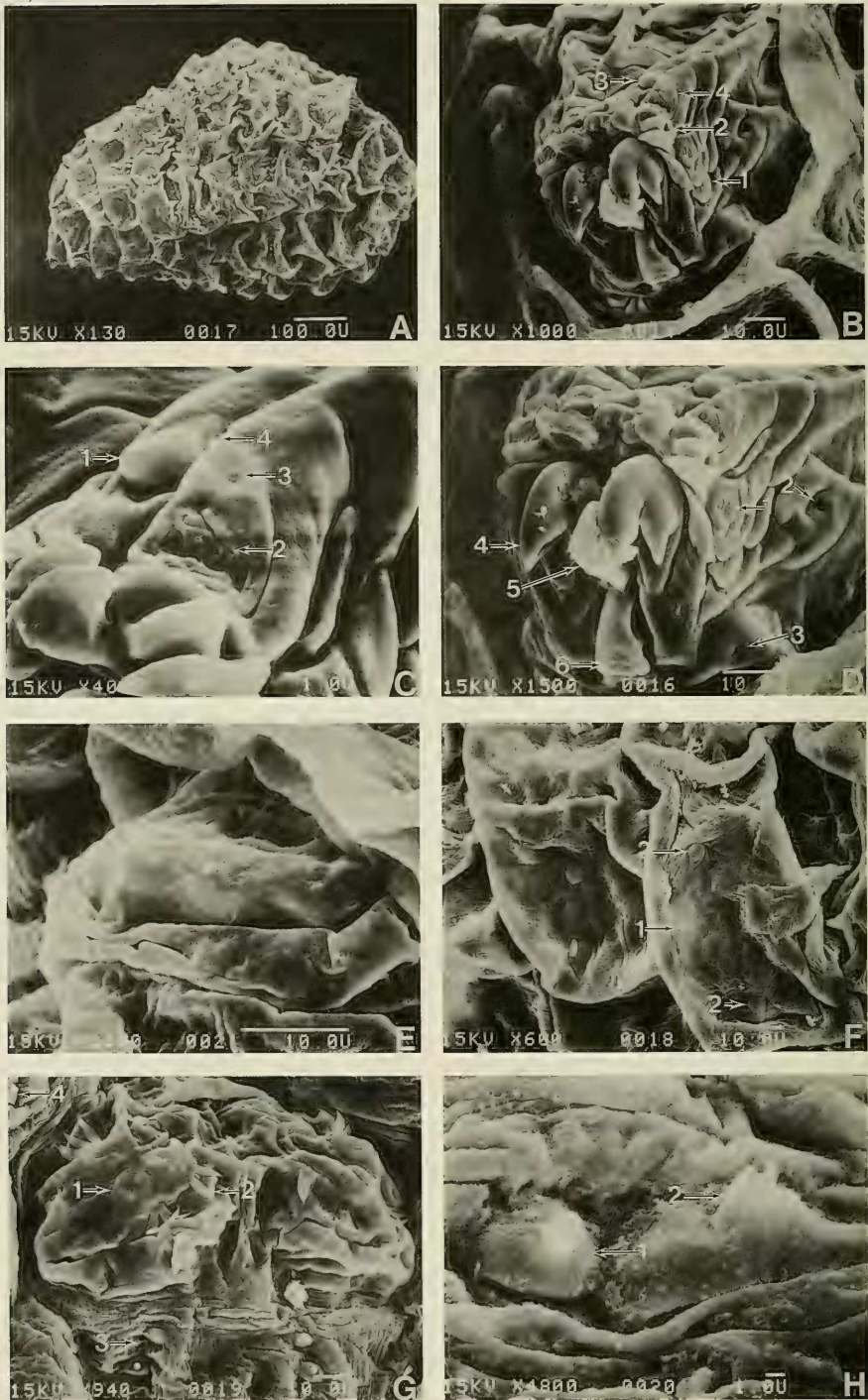


Fig. 5. Second instar of *Aciurina ferruginea*: (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—rugose pads, 2—dorsal petals, 3—dorsal sensory organ, 4—anterior sensory lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ; (D) gnathocephalon, anterior view, 1—stomal sense organ, 2—lateral sensillum, 3—ventrolateral sensillum, 4—mouth hooks, 5—median oral lobe, 6—labial lobe pore sensilla; (E) anterior thoracic spiracles; (F) mesothorax

acles are not present and the posterior spiracular plates possess only two small rimae. The lateral spiracular complex was not observed in this species but has been observed in other first instar tephritid larvae, e.g. Knio et al. (1996). The compound sensilla in the first instar larva are more distinct than in the second and third instar.

Puparium: Puparium of *A. michaeli* smooth, elongate-reniform, light to reddish-brown (Fig. 7A); anterior end bears the anterior thoracic spiracles (Fig. 7B-1), and invagination scar (Fig. 7B-2); anterior thoracic spiracles and invagination scar darkened; caudal end bears the posterior spiracular plates (Fig. 7C); plates darkened, bear three oval rimae, ca. 0.032 mm in length (Fig. 7C), and four interspiracular processes.

The puparium of *A. ferruginea* differs from *A. michaeli* in being smooth, elongate ovoidal, pale yellow, anterior end around invagination scar darkened; 100 specimens averaged 3.38 ± 0.05 (range, 2.54–4.42) mm long by 1.68 ± 0.03 (range, 1.16–2.24) mm wide (Fig. 7D); anterior end bears the invagination scar (Fig. 7E-1), prothoracic verruciform sensilla, which are lacking in *A. michaeli* (Fig. 7E-2), and the anterior thoracic spiracles (Fig. 7E-3); caudal end bears the posterior spiracular plates (Fig. 7F); plates bear three oval rimae, ca. 0.035 mm in length (Fig. 7F-1), and four interspiracular processes (Fig. 7F-2).

DISTRIBUTION AND HOSTS

Foote et al. (1993) mapped the distribution of *A. ferruginea* in North America north of Mexico to include Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming. This reflects the combined distributions of all four subspecies of *C. viscidiflorus* described by Munz (1974).

Galls of *A. ferruginea* and *A. michaeli* occur in sympatry on *C. viscidiflorus* in central and southern California, and indeed, have been found by us on the same host individuals. Swept specimens of both species of tephritids were examined from Washington during the present study, and galls of both species were pictured by Wangberg (1981) from Idaho, so these two tephritids probably occur in sympatry throughout the range of *C. viscidiflorus*. Wasbauer (1972) and Steyskal (1984) cited Foote and Blanc (1963) as the source of additional rearing records from *Haplopappus bloomeri* Gray (as *Chrysothamnus bloomeri*) and *Solidago* sp. To this host list for what was then solely called *A. ferruginea*, Steyskal (1984) added *Chrysothamnus nauseosus* (Pallen) Britton. Conceivably, *A. ferruginea* and *A. michaeli* may have different host ranges, but it is difficult to imagine that the distinctive galls of these two species, especially those of *A. ferruginea* (as interpreted in the present study), have been overlooked on hosts other than *C. viscidiflorus*. It also is conceivable that the flies reported in Foote and Blanc (1963) had been swept, not reared, or reared from *Chrysothamnus* hosts misidentified as *Haplopappus* or *Solidago*. The large genus *Haplopappus* (Munz 1974) heretofore has appeared to us to be amazingly free of tephritid galls in southern California, except for the few *Procecidochares* spp. found in flower heads currently under study (Goeden and Teerink, unpublished data). However, records for *A. aplopappi* (Coquillett) from *Haplopappus pinifolius* Gray and for *A. bigeloviae* (Cockerell) from *Haplopappus* sp. (Wasbauer 1972, Steyskal 1984) encountered during this writing render the record for *A. ferruginea* from *H. bloomeri* less suspect than the record from *Solidago*. Con-

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and metathorax, lateral spiracular complex, 1—spiracle, 2—verruciform sensilla; (G) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process, 3—compound sensillum, 4—stelex sensillum; (H) compound sensillum, 1—stelex sensillum, 2—tuberculate chemosensillum.

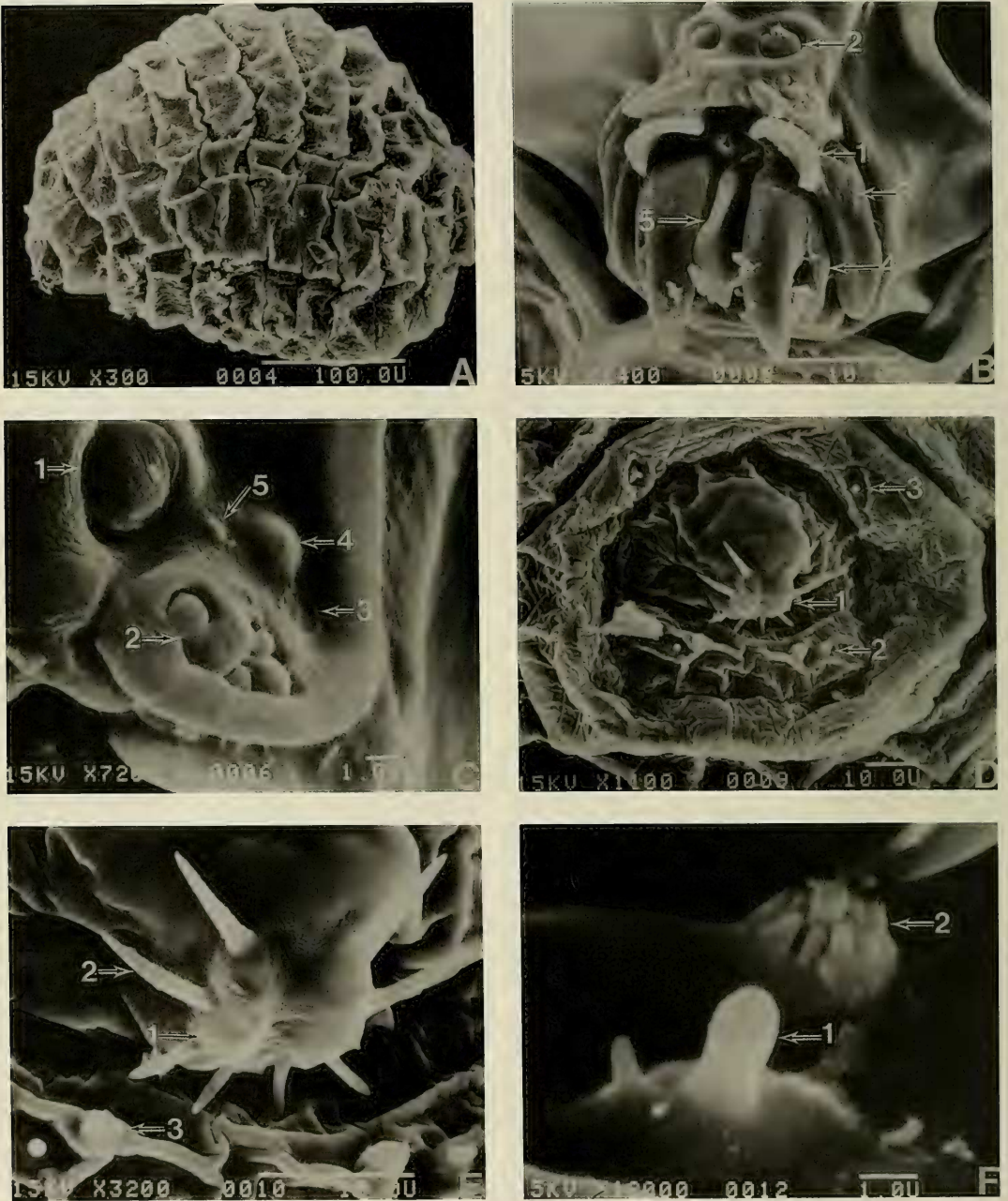


Fig. 6. First instar of *Aciurina ferruginea*: (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—dorsal petal, 2—dorsal sensory organ, 3—stomal sense organ, 4—mouth hooks, 5—median oral lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) caudal segment, 1—posterior spiracular plates, 2—compound sensillum, 3—stelex sensillum; (E) posterior spiracular plate, 1—rima, 2—interspiracular process, 3—compound sensillum; (F) compound sensillum, 1—stelex sensillum, 2—tuberculate medusoid chemosensillum.

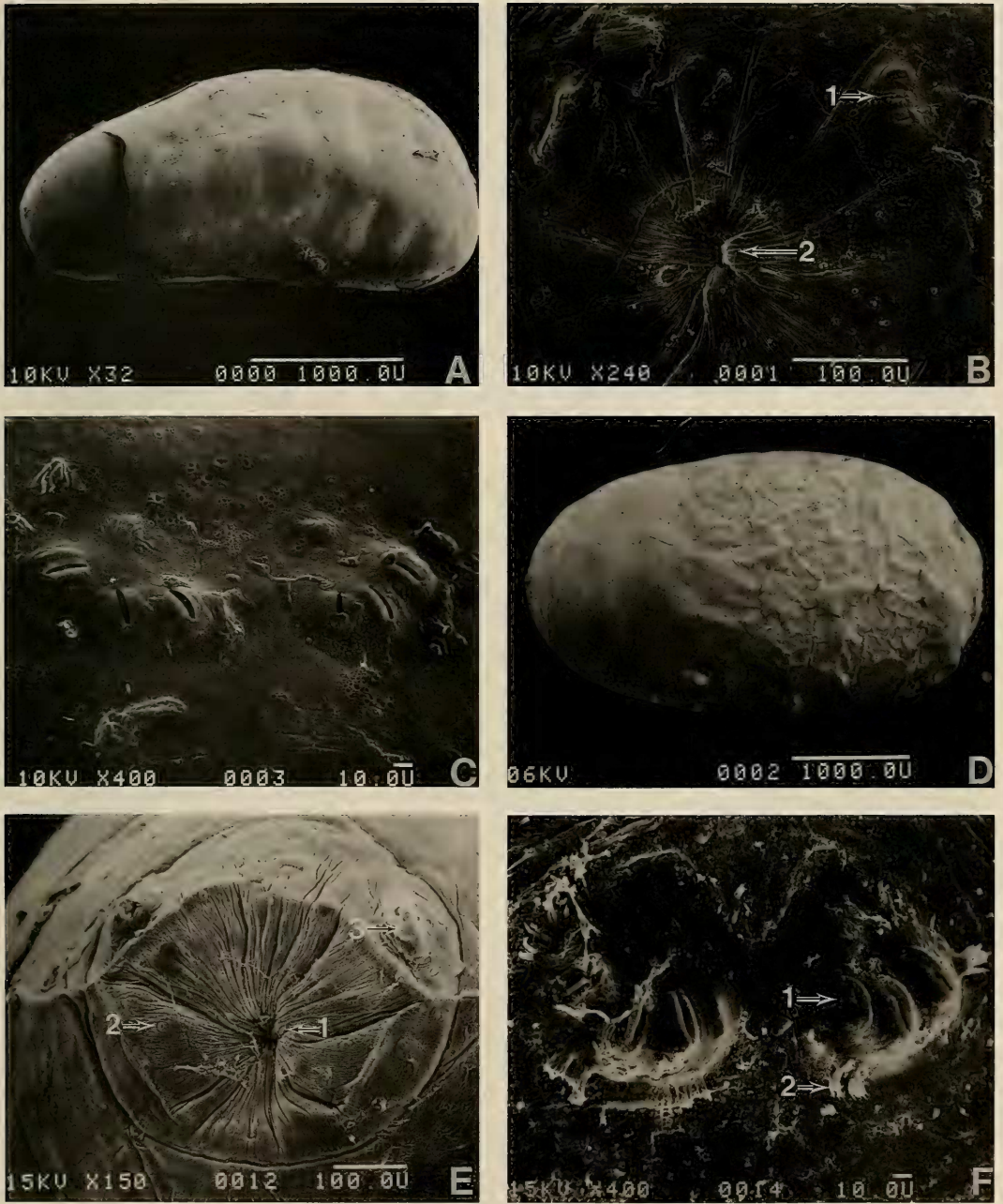


Fig. 7. Puparia of *Aciurina michaeli* and *A. ferruginea*: (A) *A. michaeli*, habitus, anterior to left; (B) *A. michaeli*, anterior end, 1—anterior thoracic spiracles, 2—invagination scar; (C) *A. michaeli*, caudal segment, posterior spiracular plate; (D) *A. ferruginea*, habitus, anterior to left; (E) *A. ferruginea*, anterior end, 1—invagination scar, 2—prothoracic verruciform sensilla, 3—anterior thoracic spiracles; (F) *A. ferruginea*, caudal segment, 1—rima, 2—interspiracular processes.

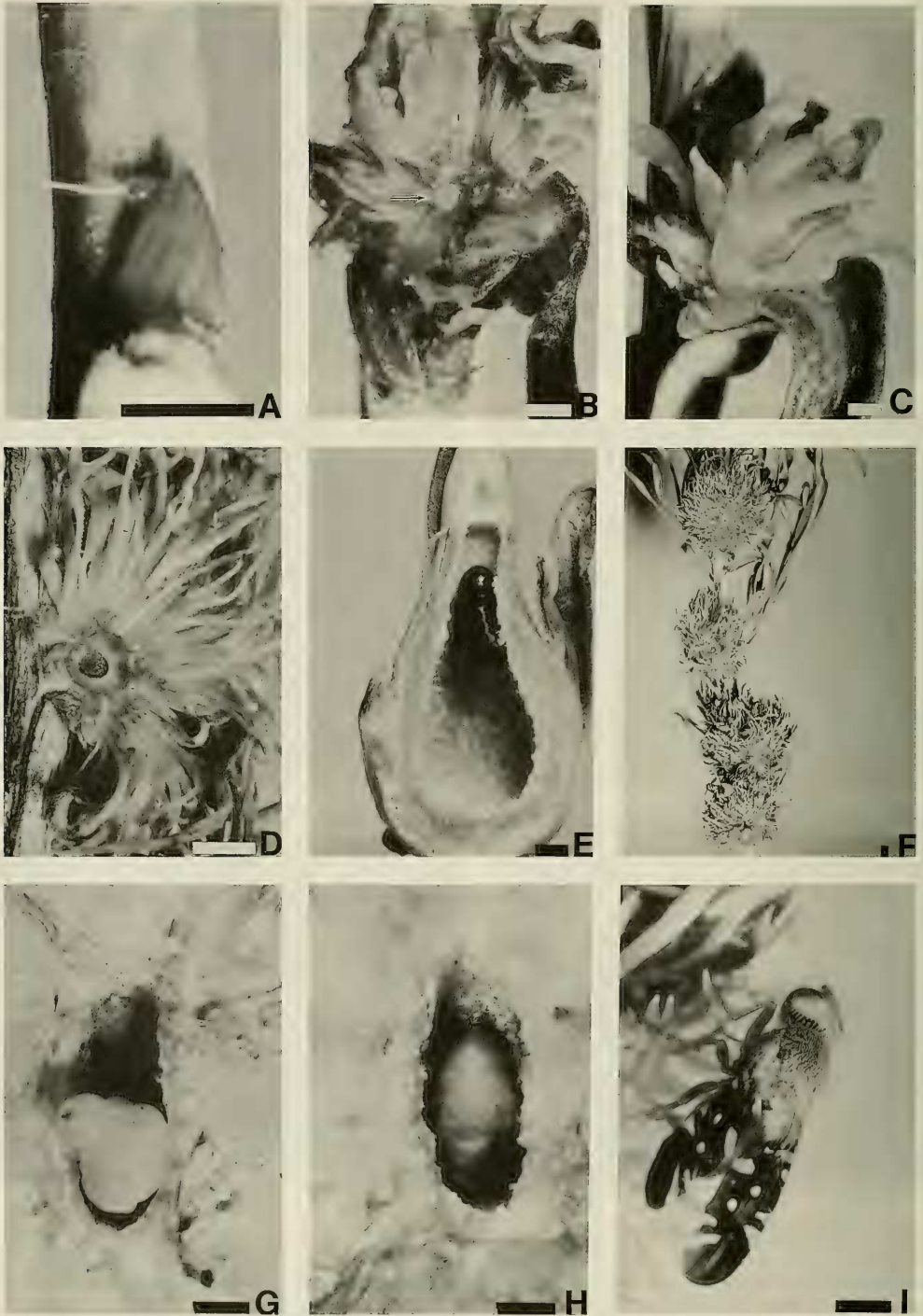


Fig. 8. Life stages of *Aciurina ferruginea* and *A. michaeli* on *Chrysothamnus viscidiflorus*: (A) pedicel and anterior part of body of egg of *A. ferruginea* projecting from axillary bud, (B) first instar of *A. ferruginea* (arrow) in early-stage gall, (C) young gall with late-first instar *A. ferruginea*, (D) sagittal section of gall containing second instar of *A. ferruginea* in locule inside basal core from which filamentous leaves arise, (E) sagittal section through mature, beaked gall of *A. michaeli* containing a puparium, (F) four mature galls of *A. ferruginea* on

sequently, we will redouble our efforts to detect their galls and rear *Aciurina* from *Haplopappus* in southern California. The host ranges of *A. ferruginea* and *A. michaeli* obviously warrant further study, but ultimately may be unresolvable, if, as suspected, they are based in part on records for misidentified host plants or flies or sweep records misinterpreted as rearing records, as sometimes confounds the literature on host plants of Tephritidae.

BIOLOGY

Egg.—Dissection of current year's flowering and vegetative branches sampled on 14.viii.1993 and 18.ix.1993 from postblossom plants bearing mature flower heads, senescent foliage, and empty, brownish, current season's galls at the study site S of Wongo Peak yielded eggs of *A. ferruginea* (Fig. 8A). But these empty galls were like those described below for *A. ferruginea* (Fig. 8D, F), not like those described and illustrated by Tauber and Tauber (1967) and Wangberg (1981), which instead apply to galls of *A. michaeli* (Fig. 8E). Adults of neither *A. ferruginea* nor *A. michaeli* were swept from *C. viscidiflorus* on either date at this location, and because this site had a light dusting of snow on the second sampling date, oviposition likely had ceased by then. The plants sampled also had been noted to bear galls of *A. ferruginea* during 1991 and 1992; therefore, certain individuals within the local host population apparently were favored for oviposition on successive years, as recently reported for *Euresta stigmatica* Coquillett by Headrick et al. (1995).

Three eggs of *A. ferruginea* were found in the sample collected on 14.viii.1993 and 12 eggs in the sample collected on 18.ix.1993. All eggs were oviposited singly in individual axillary buds (Fig. 8A). The

long axis of each egg body lay parallel to the branch or bud long-axis. The posterior end of the egg body was inserted downward between the apical pair of unexpanded leaves of a bud or between an adaxillary leaf and branch (Fig. 8A); consequently, the anterior end of the egg body and the entire egg pedicel, or the pedicel alone, were exposed and the latter part projected upward from the branch or bud apex (Fig. 8A). The eggs did not penetrate the tissues of the bud or branch. The egg bodies and basal part of the pedicel became covered with a sticky, plant-produced resin, but the upper part of the pedicel of most eggs remained free; therefore, the elongate pedicel presumably has an important respiratory function (Fig. 2B, D, 8A). Some collapsed and presumably infertile, smothered or otherwise nonviable eggs were completely embedded in the resin that covered the surface of current year's branches of *C. viscidiflorus*. This account of egg placement agrees with the description by Tauber and Tauber (1967).

Larva.—Part of the second, egg-bearing, branch sample was held as a bouquet immersed in a container of water in a refrigerator at $2 \pm 2^\circ\text{C}$ until 11.x.1994. This allowed embryogenesis to proceed slowly, evidenced by the mouth hooks seen on one embryo that had reversed its orientation 180° preparatory to eclosion from the posterior end of the egg. Moreover, three of eight (37.5%) eggs found in buds dissected on this date had hatched and the first-instar larvae had fed downwards into the buds. This confirmed that the overwintering stage for *A. ferruginea* mainly is the first instar, as first suggested by results of a series of bi-monthly samplings and dissections of developing galls conducted in 1992. Because of winter-like road conditions, we first could visit the high-altitude study site S of Wongo Peak on 22.iv.1992, fortuitously,

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single branch of *C. viscidiflorus*, (G) full-size, third instar of *A. ferruginea*, (H) puparium of *A. ferruginea*, (I) adult female of *A. ferruginea*. Line = 1 mm.

just when roadside plants of *C. viscidiflorus* were beginning to resume branch growth. Likewise, the galls of *A. ferruginea* and *A. michaeli* were just beginning to grow. All 20 incipient galls found on branches sampled on this date contained single first instars of either *A. ferruginea* or *A. michaeli*, the principal overwintering stage for both fly species. At this early stage, the galls of these species looked very similar; although, the leafy nature of the galls of *A. ferruginea* (Fig. 8B) was already distinguishable from the few-leaved, smooth, eventually "beaked" galls of *A. michaeli* (Fig. 8E). The subspherical locules in each of three galls that contained early-first instars of *A. ferruginea* (Fig. 8B) averaged 0.67 ± 0.46 (range, 0.60–0.76) mm by 0.59 ± 0.77 (range, 0.48–0.78) mm. The subspherical central chambers of 17 galls that contained individual first instars of *A. michaeli* measured 0.48 ± 0.02 (range, 0.32–0.64) mm by 0.44 ± 0.03 (range, 0.32–0.70) mm. The galled axillary buds presumably containing early-first instars of *A. ferruginea* externally measured 4.99 ± 0.96 (range, 3.77–6.89) mm long by 3.28 ± 0.40 (range, 2.72–4.05) mm wide and were located an average of 13 ± 1.5 (range, 11.5–16.0) cm below the apex of the branch on which they were formed (at the ovipositional sites). The 12 axillary buds and one apical bud presumably galled by early-first instars of *A. michaeli* measured 5.12 ± 0.39 (range, 2.51–8.0) mm long by 2.46 ± 0.13 (range, 1.67–4.0) mm; the galled axillary buds (ovipositional sites) were located 10 ± 1.3 (range, 4.0–18.0) cm below the apical bud.

The next sample collected on 7.v.1992 consisted solely of 30 *A. ferruginea* galls (Fig. 8C) each containing single, late-first or early-second instars, as by then these galls were readily distinguishable from those of *A. michaeli* (Fig. 8E), which, again, was not studied because we assumed that it was the former species that already had been studied by Tauber and Tauber (1967). Only five galls (16.7%) in this sample contained early second instars; the re-

maining 25 galls (83.3%) contained late-first instars. The next sample collected on 21.v.1992 comprised two late-first instars (12.5%) and 14 early-second instars (87.5%). Twenty-seven galls containing late-first instars from 7.v.1992 and 21.v.1992 samples, externally measured 6.0 ± 0.3 (range, 3.5–9.0) mm long by 5.8 ± 0.3 (range, 3.0–9.0) mm wide by 4.2 ± 0.2 (range, 2.5–6.0) mm thick. They were located 10.9 ± 0.6 (range, 7.0–17.5) cm below the vegetative branch apices or immature, compound inflorescences terminating some branches. By this time, the galls already appeared very leafy and consisted of stunted axillary branches, which continued to produce leaves in fascicles from many tiny axillary buds as the galls grew (Fig. 8D). The outer, nonserrate margined, linear leaves averaged 9.9 ± 0.8 (range, 3.4–18.0) mm in length and 2.1 ± 0.13 (range, 0.5–3.0) mm in width; the inner leaves, 4.3 ± 1.4 (range, 2.1–7.0) mm long by 0.6 ± 0.05 (range, 0.3–1.5) mm wide ($n = 25$). The basal locule was ovoidal in shape and 0.75 ± 0.035 (range, 0.41–1.25) mm long by 0.49 ± 0.014 (range, 0.41–0.67) mm wide ($n = 25$) by 0.36 ± 0.037 (range, 0.23–0.42) mm deep ($n = 5$). Its inner surface is shallowly pitted and thinly coated with sap upon which the larvae principally feed, as described for *A. thoracica* by Headrick and Goeden (1993). This cavity was surrounded by a parenchymatous, ellipsoidal core, 0.44 ± 0.04 (range, 0.31–0.55; $n = 5$) mm thick composed of the hollowed, laterally expanded, but shortened branch cortex within which the larvae fed, and which at this early stage of gall development measured only 1.62 ± 0.09 (range, 1.42–1.84) mm long by 1.46 ± 0.16 (range, 1.06–1.75) mm wide in cross section.

Seventeen galls of *A. ferruginea* containing late-second instars from the samples of 21.vi.1992 and 10.vi.1992 measured 9.0 ± 0.6 (range, 5.0–13.0) mm long by 9.2 ± 0.5 (range, 6.0–13.0) mm wide by 5.6 ± 0.6 (range, 3.0–10.0) mm in thickness. The smooth-surfaced, ellipsoidal, basal locule

measured 1.36 ± 0.11 (range, 0.83–2.31) mm long by 0.77 ± 0.05 (range, 0.5–1.2) mm wide in cross section, and each was surrounded by a 0.59 ± 0.03 (range, 0.42–0.86) mm-thick inner core which measured 2.39 ± 0.12 (range, 1.56–3.44) mm long by 2.00 ± 0.08 (range, 1.48–2.58) mm wide. The core bore a profusion of smooth, threadlike leaves, 7.1 ± 0.7 (range, 3.8–10) mm long and 0.65 ± 0.63 (range, 3.8–1.0) mm wide ($n = 11$). Sixteen (94%) of these bud galls were axillary; one was apical. The axillary bud galls were located 8.0 ± 0.1 (range, 3.5–16.0) cm below the branch apex or terminal, immature inflorescence.

The gall samples of 10.vi.1992 and 23.vi.1992 from the high-altitude study site S of Wongo Peak each contained two late-second instars (7%) and 28 early-third instars (93%). However, 30 galls sampled on 24.vi.1992 at lower elevations at Long Valley and Kennedy Meadows both contained mid- to full-size, third instars (Fig. 8G) and puparia (Fig. 8H) [3 (10%) and 9 (30%), respectively]. The 30 galls in the 9.vii.1992 sample from S of Wongo Peak also contained nine (30%) puparia. One hundred mature galls each containing a single puparium of *A. ferruginea* (Fig. 8H) collected from these and other locations sampled on 9.vii.1992 averaged 15 ± 0.2 (range, 12–19) mm in length and 14 ± 0.2 (range, 10–18) mm in diameter. The mean (10.7 mm) and range (6–15 mm) of 10 galls containing third instars reported by Wangberg (1981) were smaller than those that we measured containing puparia. The basal ovoidal, smooth-walled locule measured 4.69 ± 0.07 (range, 3.44–6.51) mm long by 2.03 ± 0.34 (range, 1.52–4.31) mm in diameter at one end of which the fully grown larva before it had pupariated had excavated a thin, circular, epidermal, 1.13 ± 0.016 (range, 0.86–1.46; $n = 92$) mm diam window in the otherwise 0.85 ± 0.16 (range, 0.53–1.25)-mm thick, inner core of the gall that surrounded the locule. This hard ellipsoidal core measured 5.46 ± 0.63 (range, 4.31–7.15) mm long by 3.74 ± 0.04 (range,

2.09–4.75) mm wide and bore the profusion of filamentous leaves that constituted the bulk of these highly distinctive, foliose-appearing tephritid galls (Fig. 8D, F). This gall was first described by Wangberg (1981), who apparently failed to identify the adults he “rarely reared”, and did not observe in the field, other than as “*Aciurina* sp. B”. Steyskal (1984) indicated that “Sp. B” of Wangberg (1981) “likely” was *A. idahoensis*, and conspecific with “Sp. A” of Wangberg (1981); whereas, the present study has demonstrated that the former assumption was wrong. Moreover, our unpublished data show that “*Aciurina* sp. A and sp. B” of Wangberg (1981) are not conspecific. Instead, the former species is *A. idahoensis*, which in California, though apparently not in Idaho (Steyskal 1984), has a strongly sexually dimorphic wing pattern. The life history, adults and immature stages of *A. idahoensis* in southern California will be described in our next paper in this series. The gall of *A. ferruginea* (Fig. 8D, F) is unique among those described for *Aciurina*, and apparently among other gallicous Tephritidae to date (Friedberg 1984).

Of 312 galls collected on 225 excised, current season’s branches in 1992 and 1993, 169 (75.1%) branches bore single galls; 31 (13.7%) branches bore two galls each; 20 (8.9%) branches had three galls each; four (1.8%) branches had four galls each; and only one branch had five galls. If formed on adjacent or nearby axillary buds, the leafy portions of one or more galls combined to form compound galls, within which each larva or puparium was retained in its separate locule. Accordingly, the five galls on the single branch noted above formed a single, compound gall 6-cm long.

Again, the galls of *A. michaeli* were described in considerable detail by Tauber and Tauber (1967) and Wangberg (1981) as those of *A. ferruginea*.

Pupa.—Pupariation occurs within the locule, with the anterior end of the puparium facing the window (Fig. 8H). Most locules and puparia were oriented with their

long axes perpendicular to the branches on which they were formed, but a few locules and puparia were formed nonperpendicular to the branch axis.

Adult.—The emerging adult broke through the thin epidermal window and exited the gall through an outwardly expanding, funnel-shaped channel in the leafy investiture of the gall by pushing aside and outward the leaves surrounding the window. Males were reared from galls in far greater numbers than females during 1991 and 1992, i.e. a total of 41 males to 11 females (3.7:1). Longevities of these 41 males caged in the insectary averaged 44 ± 5 (range, 4–105) days; longevities of these 11 females (Fig. 8I), 52 ± 8 (range, 2–99) days. Newly emerged females were sexually immature, but rapidly elaborated as many as 80 full-size ova in as few as 9 days ($n = 7$) after their emergence from galls.

Seasonal history.—*Aciurina ferruginea* and *A. michaeli* are both univoltine on *C. viscidiflorus* in California. Both species probably overwinter as first instars in incipient galls, similar to *Procecidochares* sp. on *Ambrosia dumosa* (Gray) Payne as reported by Silverman and Goeden (1980). However, Tauber and Tauber (1967) from egg collections like ours in September, deduced that the first instar was the overwintering stage for the species that they studied as *ferruginea*. The possibility exists that the egg eclosion that we obtained in refrigerated bouquets in October was an artifact, because we also have observed in the field that *Procecidochares minuta* (Snow) on *Chrysothamnus nauseosus* overwinters as a fully formed first instar within the intact egg chorion. Wangberg (1981) suggested that both of these *Aciurina* spp. overwintered as eggs in Idaho. Dissection of egg or first instar bearing axillary buds on previous season's branches collected in mid-winter would be the only way to settle this point of contention. Depending on which interpretation is correct, gall development begins when eggs hatch, or development of first instars accelerate, concurrently with re-

sumed host-plant branch growth in early spring (in April at our study sites). Three larval stages are followed by pupariation in late June to early July. Adults emerge in July and August, mature sexually in about 10 days, mate, then oviposit concurrently with host-plant flowering and cessation of branch elongation. Oviposition largely takes place in newly formed, axillary buds usually basally on current year's branches of *C. viscidiflorus*. This type of life history strategy involving oviposition on host plants in a suitable stage upon fly emergence has been called "circumnatal" by Headrick and Goeden (1995) and is characteristic of many, but not all (unpublished data), gallicolous Tephritidae native to California. Whether additional generations of *A. ferruginea* and *A. michaeli* are produced on other species of host plants is unknown and warrants further field study.

Natural enemies.—Wangberg (1981) reported six species of Hymenoptera parasitoids "associated with galls from laboratory rearings" of *A. michaeli* labelled, described, and illustrated as galls of *A. ferruginea* in his report: *Eupelmus* sp. (Eupelmidae), *Eurytoma* sp. (Eurytomidae), *Halticoptera* sp. (Pteromalidae), *Tetrastichus cecidophagus* Wangberg (Eulophidae), *Torymus* sp. (Torymidae). He also reported the following Hymenoptera as associated with galls of *A. ferruginea* (his *Aciurina* sp. B) from rearings made by E. J. Allen in 1966: *Eupelmus* sp., *Habrocytus* sp. (Pteromalidae), *Torymus* sp., and *Zatropis "albiclavatus"* [*alboclavus* (Girault)?] (Pteromalidae). We, in turn, have reared the following parasitoids in southern California from *A. michaeli*: *Baryscapus* sp. (Eulophidae, Tetrastichinae), a gregarious, primary, larval-pupal endoparasitoid; an unidentified Tetrastichinae, a gregarious, primary, larval-pupal endoparasitoid; and two *Halticoptera* spp., as primary, solitary, larval-pupal endoparasitoids. From *A. ferruginea*, we reared the same two *Halticoptera* spp. and an unidentified, primary, solitary, larval ectoparasitic Torymidae. The two *Halticoptera* spp. were

by far the most common parasitoids reared from both *A. ferruginea* and *A. michaeli*.

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